Volume VIII. *August, 1893.* *Number 3.*

JOURNAL

OF

MORPHOLOGY.

THE AUDITORY OR HAIR-CELLS OF THE EAR AND THEIR RELATIONS TO THE AUDITORY NERVE.

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The present condition of this question, so far as the Golgi method has influenced it, may be epitomized as follows:

1. The hair-bearing or acoustic cells of the ear are not nerve cells; but they represent a secondary and higher differentiation of the nerve end apparatus.

2. All fibres of the auditory nerve are apparently outgrowths of the bipolar ganglion cells, one process reaching to the periphery, the other into the central nervous system. The peripheral processes sometimes terminate in small knobs below or among the hair cells; but more frequently they end in numerous fine branches which pass up among the cells and often reach quite to the surface of the epithelium.

3. All the cells of the several auditory ganglia are simple bipolar ganglion cells and are considered to retain a more primitive condition than the ganglion cells of the spinal ganglia.

4. The acoustic cells are not homologous with olfactive cells since although hair-bearing they are not continuous with the nerve fibres and are only secondarily brought into relation (not more than a mere contact) to the free ends of the auditory

nerve to serve in the place of the primitively superficial cells (ancestral hair cells) which have become the bipolar cells of the auditory ganglia.

5. The system of spiral nerves is composed of fibres within the *cochlea* which run at right angles to the radial fibres and may or may not be all derived from the radial fibres. Very probably not, as all previous investigators who have accepted the spiral system, have maintained.

These are the conclusions of Retzius and Van Gehuchten the only investigators who have published results of the application of the *Golgi* method to the whole ear. The nerve ends of the maculae and cristae have been studied by another investigator, O. Kaiser, who has described the nerve-end as having the form of a calyx, like an egg cup, into which the hair-cell fits.

In using the Golgi method on the mammalian ear, I have found that success was obtained only when two conditions were observed. The tissue must be free from calcareous matter either in solution or in deposit and it must be placed in the osmium-bichromate mixture alive. Successful stains do not always reward this care, but of other precautions I have no very definite knowledge. These remarks apply to the ear of the sheep, ox and pig in adult condition, and to the ox and pig in embryonic stages, and in this case mainly to the pig. The best results were obtained from embryos of 8–14 cm. length as the creatures lie on a scale. The ears were carefully removed from the head, cleaned of superfluous tissue and put at once into a solution of $Os. O_4$. 1 per cent 100 cc. + $K._2\ Cr._7\ O._7$ 500 cc. As from 100 to 200 ears were prepared at a time, the work of preparation was shortened as follows. The heads were removed from the embryos to the desired number, then all were sagitally bisected and the brain removed and a third operation shelled out the internal ears which in embryos of this size are still entirely cartilaginous. From 50 to 100 ears were placed in a low but large mouthed bottle of circa 200 cc. capacity, and first well washed off with osmium-bichromate solution once used, which was replaced after a little gentle shaking by a bottle full of the fresh solution. In this the ears remained for 24 hours without change unless the liquid grew turbid. As a rule one change is required. Having tried various *times*, from 16–56 hours, I find that if the ear stains at all, it will do so after a bichromate bath of 24 hours, and as a rule anything less gives an incomplete stain. More variation in the stain is produced by varying the time of the silver bath, but a good and uniformly satisfactory period was found to be 24 hours. Successive transfers, from the silver bath back to bichromate, were not productive of any completer stain than had resulted from the 24 hours of immersion in the bichromate and silver baths respectively. Two strengths of silver bath were used, 0.50 per cent and 0.75 per cent. If there was any difference it was in favor of the stronger solution. The silver bath was changed as often as it became turbid from suspended crystals, and ears were washed in used silver bath before being put in the full strength solution.

The penetration of the solutions is aided materially by increase in temperature, and a warm oven may be used with advantage, though it is not necessary.

It may be well to repeat that where calcareous matter was present in the ears they uniformly failed to stain, and I consider the bone tissue of the adult ear the main source of trouble in attempts to stain the adult cochlea by the Golgi method. It acts as a sure *preventive* as the method is now applied. The following paper is descriptive of Golgi preparations, and the conclusions possess only the weight which belongs to this important method. But it must be borne in mind that while this silver stain reveals details of structure in complicated arrangements with a distinctness unsurpassed, it at the same time conceals some of the relations of the very things so clearly set forth.

A. *The Hair cells of Corti's Organ or the Mammalian Cochlear Organ.*

The organ of Corti is a very complicated structure, but it has received during its differentiation no new elements, for the arch of Corti is not to be looked upon as a new structure, but rather as a modification of elements present in all the sense organs. Golgi preparations show many degrees of staining of the cell elements of the organ. In those stained the least, only nerve fibres are visible and these, few in number, are found in the cochlear axis and in the lamina. The supporting cells of the organ are next in order to take the stain, after which come the ganglion cells of the cochlear ganglion, and finally the hair-cells themselves. When the stain is abundantly deposited all detail is lost or rendered valueless, but where the happy mean is observed, hundreds of isolated cells are stained, and many of them show the nerve endings clearly defined. The hair-cells in such preparations show a subglobular or a pyriform body, on the top of which the hairs are only occasionally stained (Pl. I, Figs. 5 and 7). From the centre of the base of each hair-cell issues a nerve fibre which, in a favorable case, admits of being traced through a ganglion cell of the cochlear ganglion into the collection of fibres which pass on to the brain (Pl. I, Fig. 2). These fibres are by no means simple straight threads, but show many varicosities in their course from the hair-cells to the brain, the largest of which are near the hair cells of the organ of Corti, but within the territory of the Sauropsid organ (Pl. I, Figs. 2, 4, 5 and 7; Pl. II, Figs. 8–11, 15 and 17; Pl. III, Figs. 25 and 27). These varicosities vary greatly in size. The most numerous are slight enlargements in the course of the nerve thread, and are more frequently oval than spherical, but they may appear angular as the stain brings them to view. This kind of varicosity occurs in all parts of all the nerves of the ear. Another sort of enlargement consists of medium sized spherical swellings of the fibres or of their branches, and are especially numerous in the organ of Corti upon the short branchings of the nerve. They more especially belong to the "connective" fibres or hair-cell commissures which run along below each row of hair-cells for unknown distances, and enlarge below each cell into subglobular beads into which as a rule the fibres from the hair-cells penetrate. The largest varicosities are scarcely inferior to the ganglion cells in size but unlike most of the latter, several or many processes radiate from the body of the enlargement. These bodies occur with considerable regularity, so that in surface preparations of the organ of Corti and, better still, in horizontal sections of the same, a row of the inner hair-cells is accompanied by a row of these large varicosities. I am undecided what their true nature is. One is not able with this method to determine their cellular nature, and I have no observations on this point by means of other methods which it is desirable to publish now.

A point of importance I shall mention here, though it does not belong strictly to the nerve endings. As I have already stated, the hairs on the acoustic cells of the cochlea seldom show in well stained preparations, though they frequently do in those incompletely stained. This is due to the shortness of the ends left on the cell caps, and the enclosure of these short ends by the silver deposit. In the case of the maculae and cristae the hairs do not as a rule break off, and when they do they leave a relatively large and long conical hair remnant which is not covered by the silver precipitate to such an extent as to hide the nature of the process. The hairs of the maculae and cristae are very well defined by this method, and appear about *twice as long* as by the ordinary methods of staining with balsam mount. The relation of these hairs to the otoliths I shall describe in another communication.[1]

Returning to the hair cells, we find that the nerve processes which leave them are not always simple, but often branching threads as the Golgi stain shows them. The branches anasto-

[1] In Fig. 24, Pl. III, I have sketched the stained hairs of a portion of the organ of Corti in a 20 cm. pig embryo. First of all one will notice that the hairs are not arranged in the form of a horseshoe upon the top of the cell, but they cover a more or less regular and approximately circular area. Between the row of dots marked 1 (inner hair-cells) and the row marked 2 is found the crest of the Cortian arches. The following rows are quite complete throughout all parts of the cochlea until we arrive at the fifth row which occurs for short distances only along the middle spiral turn and the distal and proximal parts of the basal and apical turns respectively. Golgi's method brings out the presence of these hairs with a clearness of definition shown by no other method. It may be noted in passing that the caps of the supporting cells are not in the region of the fifth row sufficiently well developed to form the figures composing the "reticulate membrane." Pl. II, Fig. 15, shows the appearance presented by an isolated hair-cell defined among the stained rows of hairs.

mose with the processes from neighboring cells and thus form a delicate plexus of fibres where the anastomoses are numerous, Pl. II, Figs. 11 and 17, Pl. III, Figs. 25 and 27, will serve to give a faint idea of the character of this plexus. In Fig. 27, Pl. III, the sub-epithelial commissure (*c*) is shown, while in Fig. 25 there is depicted a few meshes of the plexus connected with one of the commissural varicosities (*v*). From each of the varicosities pass off two sorts of fibres. Those which form part of the plexus, and those which serve to connect the hair-cell with the varicosity. Of the former sort are the "spiral fibres" which enter the plexus. Only a few of the spiral fibres are thus engaged.

B. *The Radial Nerves.*

When the cochlea is viewed perpendicularly to its helical axis, the greater number of the nerve fibres, leaving the organ of Corti, run nearly at right angles to the tangent of their point of origin into the cochlear ganglion, and thence toward the helical axis, about which all the fibres are spirally twisted as they descend to the base of the helix (Pl. I, Fig. 1). Some of the fibres, between their hair cells and ganglion cells, suffer displacement in the horizontal plane, which often nearly doubles their length between these two points.

Lateral displacement in this plane occurs in greatest abundance in the organ of Corti (Pl. I, Figs. 4 and 7; Pl. II, Figs. 8, 13 and 17; Pl. III, Figs. 18, 19, 22, 23, 27 and 31), next in the region of the *Lamina ossea*, and least of all — though still to a considerable degree within the cochlear ganglion itself, where it gives rise to the appearance of bands of spiral fibres (Pl. I, Fig. 7s, and Pl. II, Fig. 12, spiral fibre), much the same as within the cochlear organ itself. The bundles in the ganglion are larger than those of the organ of Corti, a character not shown in the figures where only a single fibre is drawn in.

When viewed at right angles to the vertical or helical axis the nerve fibres form a series of incomplete funnels with the hair-cells as their thickened borders. This appearance is due to the fact that the fibres leave the organ of Corti in a nearly continuous sheet, which stretches downward and inward, at an angle varying with the spiral gradient, until it fuses with the central core of nerve fibres.

Many of the individual nerve fibres suffer displacement in the vertical plane, both upward and downward, from the plane of the sides of the funnel, the greatest amount of displacement occurring near the ganglion (on either side) and in the region where the fibre is suddenly drawn into the vortex and spun onto the helical core. The fibres may cross the planes of each other's paths several times between the hair-cells and ganglion (Pl. I, Fig. 1).

Besides the pictures presented by the three views above described we have still to consider the fibres to be best seen in surface view of the organ (they appear in side view only in transection and consequently as black dots). These fibres are of two sorts (*a*) those simple radial fibres which, having apparently lost their way when growing toward the modiolus, have pursued a circuitous course before finding their destination, and (*b*) those fibres which arise as collaterals of the radial fibres and run for greater or less distances in more or less "spiral" direction in the lamina ossea, both within the cochlear ganglion and in the plate of nerve fibres of this lamina (Pl. I, Figs. 4 and 7), and finally the third kind (*c*) composed of the peripheral branches of radial nerves due to the division of the hair-cell without the accompanying partition of its nerve (Pl. II, Figs. 8, 9, 11 and 17; Pl. III, Figs. 24 and 27). In making a distinction between the kinds *b* and *c*, and in calling the former "collateral," I have not attempted to make a distinction based on true morphological grounds, but to direct attention to an *apparent difference* which may, in reality, be due to the same process of growth, about which in the present communication nothing more need be said.

I will add here that the varicosities on the nerve fibres in all parts of the ear appear to be cellular in nature. This does not appear from the Golgi method, nor is it apparent in the case of the finer nerves with any of the ordinary methods, but in Methylen-blue preparations I have yet to find an enlargement of an axis cylinder due to an increase in size of that structure itself. What appears to be of such a nature in Golgi preparations is in reality due to the presence on the fibre of cellular structure, which in most cases is a sheath nucleus, resp. sheath cell.

The details and illustrations I contemplate publishing in the near future.

C. *The so-called "Spiral Nerves."*

The system of spiral nerve fibres in the organ of Corti (only), which was discovered by F. E. Schulze, very fully described by Deiters in 1860, and which since that time has been variously identified and described by many others, is clearly defined by the Golgi method, and its claims to an independent position not sustained. This "system" of spiral nerves proves to be nothing more than portions of the radial nerve system drawn out of the radial course into oblique or short spiral courses, and is not, as previous writers have left us to infer, confined to the organ of Corti alone, but occurs frequently between the modiolus and the end organ. The most clearly defined bundle of such spiral fibres occurs in the cochlear ganglion (Pl. I, Figs. 4 and 7; Pl. II, Figs. 8–10, 11 and 12; Pl. III, Figs. 18, 19, 22, 27 and 29).[1]

In the case of all spiral fibres, where the fibre could be traced, the emergence of the fibre from the ganglion as a genuine radial prolongation of a ganglion cell, was found to obtain without exception. The reason why the spiral fibres exist is because during the growth of the fibres from the hair-cells toward their central connections, they grow away from the cells along the paths of least resistance, with, however, a constant tendency to enter the central nervous system. There are, apparently, only two ways in which a nerve fibre may be laid down between the cell of origin and the brain — (*a*) each cell may send its process, as a distinctly individual outgrowth, to the brain, or (*b*) all cells of later generations — derivative cells — may acquire more or less of their central process by a splitting of the fibre already belonging to the parent cell. This latter method is probably the one which takes place most

[1] Henle has figured one of these bundles as a part of the cochlear ganglion.

frequently, and on this assumption the intricacies of the innervation of the auditory sense organs are readily explained. When a fibre from one of the outer rows of hair-cells starts on its journey to the brain it meets obstacles of several kinds, and all along its course, so that the direction it is to take is very much a matter of accident. One process of development, above all others, determines its general course. I refer to the spiral growth of the cochlea, which, during this period, is actively going on, so that all fibres have this spiral twisting force exerted upon them, and it results in giving many of them a curved, if not spiral, course to the modiolus. As growth goes on the cell is carried away from the position occupied at the time when it started its cell process, and in this way the convexity of the curve of the fibre is turned away from the direction of growth. If the cell process fails to find passage-way through a cell-row, or past any other obstruction, it may be turned either way and grow for a greater or less distance before proceeding further radially. A fibre may suffer such an interruption of its course several times before it passes out of the organ of Corti. Another source of displacement and plexus formation, is this — after a fibre is once laid down the cells between it and its point of passage through the hair-cell row or rows may increase in number, and force the nerve fibre to grow in length in this part of its course, so that, ultimately, what was at first only a short bend in the nerve fibre becomes a long "spiral" thread.

The so-called spiral nerve tracts of Corti's organ are, in some cases, the product of the *lateral branches* of the cochlear nerve before leaving the organ (Pl. I, Fig. 5, *sp.*; Pl. II, Figs. 11, 17; Pl. III, Figs. 25, 27). The main (system) collection of these fibres is found below and inside of the inner hair-cells, *i. e.*, in the lymph space generally formed in this region, and which has been named Nuel's canal, a name which there is no necessity for retaining. In preparations of the fresh organ of Corti, this lymph space, with its contained structures and many of the adjacent cells, comes out as a long cylindrical structure, having the appearance shown in Pl. III, Fig. 10, of my Vertebrate Ear Memoir. On Pl. III, Fig. 28, I have sketched the appearance of a portion of the nerve bundle within this lymph space, as defined by the Golgi stain.

D. *The Foramina nervina of the Habenula perforata.*

All previous observers have described the holes in the habenula perforata as slit-like or oval openings, and there is a unanimity of opinion (supposed to be fully justified by repeated observations by scores of observers) that the auditory nerve enters the cochlear canal in regular bundles through these holes.

It is true some observers have laid special stress upon the fact, admitted by all, that among birds and reptiles the nerves emerge from the basilar membrane, not in bundles, but singly, and also that in the upper end of the organ of Corti in Mammals the same method of entrance exists.

I held the same views until Golgi preparations taught me better. The bundles of nerve fibres from the cochlear ganglion, as they approach the habenula perforata, are not so compact as they appear in ordinary preparations of the cochlea, for the silver stain shows that there are no sharply defined *foramina nervina* for bundles of nerves, but that only an approximation to this condition obtains, while many nerve fibres may enter the cochlear canal between any two fibres of the basilar membrane, which are thus separated and which may be said to form the boundary of their foramen. Many of the nerves will be found to pass between other fibres of basilar membrane in such a way as to produce irregular groups of fibres (Pl. III, Fig. 32). In Golgi stains of this region, with the organ of Corti removed, the broken nerves appear as dots, and an inspection of Fig. 32 will make it clear that there is nearly a continuous series of fibres which find their way through the basilar membrane. Periodically reinforced by larger bundles of fibres more or less closely packed together, this nearly continuous series of fibres (the Sauropsid condition) assumes the appearance of a series of separate groups here and there continuous and with a tendency (everywhere shown) to fuse together.

E. *The Nerve Fibres in the Lamina ossea.*

The course of the fibres of the cochlear nerve in the *Lamina ossea* I have already given, but of the characters of the bundles of nerves within this region I can say little. On Pl. III, Fig. 19, are shown several bundles of fibres in this region. The figure illustrates how the fibres group themselves in bundles, leaving elongate interspaces between the bundles quite as well as any of the Golgi preparations show it, but I shall reserve for my paper on the results of the Methylen-blue stain a complete account of the structures occupying the *Lamina.*

The same causes seem to operate here that are so effective in the organ of Corti, to turn fibres out of their direct course, and as a result there is an extensive "anastomsosis" of bundles.

Part of this interchange of fibres is a simple displacement of fibres from a direct path, but apparently another part is of a much more important nature, and consists in the connecting together of different parts of the cochlear apparatus nervously, and in this way, of course, connecting many or few, more or less widely separated peripheral points in the cochlear percipient organ with single points in the central nervous system. Collateral fibres are frequent in the region of the *Lamina ossea,* but whether they occur as abundantly centrad of the ganglion I have not been able to determine. They do occur, but heretofore they have only been seen in a few instances.

F. *The Auditory Ganglia especially the Ganglion cochlearis.*

The ganglion cells of the cochlear ganglion take a very prominent place in the discussions of ear anatomy at the present time and their origin and nature is a matter of much importance to the proper understanding of the structure and workings of the acoustic appartus. Retzius and van Gehuchten unhesitatingly say that all the cells of the cochlear ganglion are bipolar cells from which the two fine nerve filaments take their rise, one going to the periphery as the hair-cell element the other going to centre as the brain element. At either end the nerve is supposed to end freely and to acquire relations to other nervous structures by mere contact at the very most. Their views are not sustained by the facts of adult anatomy. It will however be impossible to throw satisfactory light upon this matter until the development has been worked out with completeness. It may not be a waste of words to record the following conclusions which have grown out of my study of the innervation of the ear. Although tentative they have the harmonious support of the facts of adult anatomy and involve at the same time an explanation of the histogenetic processes which is entirely probable on account of the fact that the nerve process is continuous with the hair-cell (this point I have just recently verified by the Methylen-blue method which gives the needed histological details of the continuity wanting in the Golgi preparations) and we may thus hold that the hair-cell is a genuine nerve cell and the cell of origin of the auditory nerve fibre. The ganglion cell which lies at a distance from the hair-cell in the *canalis ganglionaris* of the adult was at the very least, in contact with the hair-cell at an early stage of its development for the ganglion is continuous with the superficial layer of cells of the embryo which become the superficial hair-cells of the adult. As development pro ceeds we know that the ganglion recedes further and further into the head until it reaches its adult position. My assumption is this — during the multiplication of the sense organ rudiment in early stages, the ganglion cells are the product of the division of the superficial hair-cells, and as development proceeds the protoplasmic bridge left over from an incomplete cell division is drawn out into a fine thread — the fibre which crosses the lamina of the adult. Either before or soon after this bipartition of the primitive sense cell began the centrad process started for the brain from the proximal end of the primitive sense cell which of course, in the adult, remains the proximal end of the ganglion cell. In case of the division of the superficial hair-cell the impulse[1] generated in it would of course travel to the other end of the cell and cause a like division of the ganglion cell so that we should expect to find bipolar cells in the ganglion, and they are there in abundance. But we also find many multipolar cells whose presence is only

[1] Impulse to division in a plane at right angles to the first division.

to be accounted for by supposing that the impulses to division sent onward from the periphery have not influenced the ganglion for some cause not now conspicuous. And finally, some of the divisions do not reach the ganglion cell, and thus give rise to branching fibres between the ganglion and hair-cells. As a result we would get from this process exactly what we find in the ganglion and organ of Corti, *viz.*, a single ganglion cell with two or more hair-cells connected with it by nerve fibres while only one nerve fibre proceeds from the ganglion cell to the nerve centre.

Most of the complicated figures and groups formed by hair-cells and nerves in the organ of Certi lend themselves to this explanation while I have failed to find any other satisfactory view applicable to the sensory structures of the whole ear. Only a detailed knowledge of the histogenesis of this organ can determine the full story of this process.

The cochlear ganglion (Pl. I, Fig. 1), is an elongate cylindrical body, spirally twisted to fit the helical inclination of the proximal portion of the lamina ossea which is here channeled by a lack of ossification. This *canalis ganglionaris* or Rosenthal's[1] canal of the human ear, is marked by the successive enlargements and constrictions of the cord of ganglion cells and nerve fibres which it contains and which really represents a chain of ganglionic bodies. A radial section passing vertically through the helix and through one of these enlargements shows the maximum size of the ganglion. The cells are quite regularly distributed through the body of the ganglion and are separated by the passing nerve fibres and the network of blood capillaries which riddle the ganglionic body, and which unite with a more compact vascular network forming a cover to the mass of ganglion cells. Most of the ganglion cells are bipolar, but multipolar cells (Pl. II, Figs. 12 and 13), are not uncommon (3–6 processes). Most bipolar cells have the nerve fibre running through them radially as this is defined above, but others are so placed that the fibre passes not directly out of the ganglion, but follows along in among the cells in one of the two directions, to sooner or later emerge from the body and make

[1] By an inadvertence this was printed Rosenberg's canal in my recent memoir.

its other connections. These may be called the spiral nerves of the ganglion.

The multipolar cells receive several radial fibres and unite them into one body and give issue to only one central fibre which may in its turn receive a collateral which passed the ganglion cell or split off from the ganglion cell so as to appear to arise from the centrad fibre (Pl. II, Fig. 12, 13). Not all of the fibres running to the periphery arise from the cell body since some of them may form by the splitting of the cell process even at a considerable distance from the cell.

The whole question on both sides may be summed up in these words. Both sides claim that the bipolar (and multipolar, Ayers) ganglion cells have contact both with the periphery and with the central nervous system. European investigators claim that although the bipolar ganglion cell was originally the superficial hair bearing acoustic cell it has gone below the surface by elongating its body peripherally into a long nerve filament which enters into relations with other superficial cells which have become hair bearing acoustic cells, while I claim that these investigators have overlooked the continuity of the bipolar ganglion cell with the hair-cell and that in consequence of this continuity we must still look upon the surface cell as one-half of the primitive acoustic cell and the bipolar cell as the other half which by incomplete cell division has become spatially separated from its congener though still structurally continuous with it. And I further claim that only on this assumption can we explain the many peculiarities of the finer anatomy of the auditory sense organs which their theory fails to elucidate. Ontogeny alone can decide this question.

G. *The Sauropsid Organ.*

The evanescent auditory organ which I have described for mammalian embryos has a very interesting history with regard to its innervation. At a time when the organ of Corti is still very small the Sauropsid organ has reached its greatest development and most of the nerves which pass into the cochlear ganglion really arise from its epithelial cells. The cells having continuity with the nerve fibres are in many points unlike the hair-cells of Corti's organ, but they are probably, in essentials, the same. A detailed account of them I shall not attempt here but reserve for a later publication. Before adult life is reached this entire organ is resorbed and its place is marked in the mammalian cochlea by the *sulcus spiralis internus*. Its peripheral hair cells and their central prolongations, with their connections being thus annihilated must leave important changes in the nervous constitution of the growing mammal the history of which has yet to find a student.

In Figs. 20 and 21, Pl. III and in Fig. 1, Pl. I are shown the peripheral nerve branchings in the Sauropsid organ. The continuity of the hair cells of this organ with the nerve fibres is given in Pl. I, Fig. 3, where the cells are seen to be different in shape from those of its offspring the Cortian organ. From all I have seen thus far, however, I am inclined to the view that the two apparently different cells are essentially alike, but no definite conclusions can be drawn from Golgi pictures alone. After leaving the hair-cell the nerve (Pl. III, Fig. 21) runs directly to the basement membrane of the organ — *membrana basilaris*, and after piercing it bends suddenly inward on its way to the ganglion. Varicosities occur all along the course of the fibres but they are more numerous peripherad of the ganglion than centrad of it. This statement is true for all classes of vertebrates. Here as in the Cortian organ they are found close up to the hair-cells and in case of the fibres from both organs they occur in contact with the ganglion cells. In describing this organ as an embryonic sense organ in my recent paper I had not been able to satisfactorily determine that its cells received nerve fibres in the mammal. I was able to do so however in the case of its homologue in the Alligator. Under the circumstances it is a pleasure to add this further point to our knowledge of the race history of the mammalian stock and another important problem to the endless list already before morphological workers for solution. From an examination of Retzius' figures and Van Gehuchten's account of cochlear innervation I have no doubt that a part of what they have described as nerves in the organ of Corti are really nerves in the Sauropsid organ, and until they distinguish clearly between these structures (the latter of which as yet they do not appear to recognize at all) they are sure of perpetuating some of the errors they have already published.

H. *The Maculae and Cristae, especially the Macula sacculi.*

The hair-cells of the maculae and cristae are readily stained in continuity with their nerve fibres and the conditions are not fundamentally different from those described above for the hair-cells of the cochlea, though the relation of the parts in the maculae and cristae is simpler and more primitive, and deserves careful study on this account, since it enables us to better unravel the intricacies of cochlear anatomy. The acoustic cells Pl. II, Fig. 16; Pl. III, Fig. 29, reach only about half way from the epithelial surface to the basement membrane and the nerves from these cells pass, of course, interepithelially downwards and through the floor of the sensory structure and form into the nerve trunk of the same name as its respective organ. Ganglion cells have not been stained on any of the fibres from the maculae in my Golgi preparations and I notice Van Gehuchten has had the same experience. There is however no reason to doubt their occurrence here and Retzius records finding them by this method. In most sections (perpendicular to the surface) of the maculae acusticae (specifically in this instance Mac. ac. sacculi) the hairs from the tops of the hair-cells are more or less bent, oftentimes considerably so, by the contraction and consequent greater pressure of the otolithic mass upon the surface of these organs, as is illustrated in Pl. II, Fig. 16 and Pl. III, Fig. 30 b. In such cases the length of the hairs on the cells is *seen to be double that usually obtained by measurement after removal of the otoliths.*

In Pl. III, Fig. 29 I have sketched with aid of a camera some of the stained nerve fibres and bodies present in a thick section of the saccular sense organ of the pig of 14 cm length. There are three points here shown which are of frequent occurrence and therefore usual and normal and which appear to be of importance in comparison with cochlear anatomy. At the bases of the hair-cells among the nerve fibres relatively large bodies certainly cellular in nature occur. They have many fibres running from them. These same figures are seen in cochlear preparations lying among the supporting cells at the bases of the hair cells. The fibres of the saccular nerve do not always leave the organ as simple fibres but frequently as several branches which soon unite into a single fibre, and finally there are numerous fibres in the simpler sense organs of the ear which take a course at right angles to the long axes of the sense cells and run through the epithelial tissue of the organ for considerable distances. They are varicose fibres showing occasionally collateral branches and they sooner or later bend upward to end in hair-cells or downwards to unite with some other fibre on its way out of the organ, or to make a separate exit by itself. To my mind they are the homologues of the "spiral fibres of the Cortian organ.

In view of the facts above recited we may fairly conclude:

1. That hair-cell and bi- or multipolar cells of the cochlear ganglion — are both parts of a single morphological unit — the *acoustic element* which mediates between points at the surface and points in the nervous centre.

2. That there is no fundamental difference between the acoustic and olfactive elements yet made known.

3. That all fibres of the auditory nerve proceed out of hair-cells alone so far as has yet been satisfactorily determined.

4. That the so-called spiral fibres are but parts of individual radial fibres bent to a right angle, more or less, out of their course. They are in some cases the product of the lateral branches of the cochlear nerves within the organ of Corti, the region of the lamina or the cochlear ganglion itself.

5. That in the mammalian embryo the auditory nerve is at one time mostly composed of nerve processes arising in the Sauropsid organ, and that as this organ fades away and the mammalian organ increases in size the nerve becomes more and more a bundle of fibres from the acoustic cells of this latter organ.

6. That so far as we yet know there is no special significance to be attached to the fact that the majority of the cells of the cochlear ganglion are "bipolar" though intermixed with an important minority of multipolar cells of from 3 to 6 processes.

THE LAKE LABORATORY,
MILWAUKEE, Jan. 5, 1893.

EXPLANATION OF THE FIGURES.

Unless otherwise stated, all figures are from preparations of foetuses of Sus scrofa domestica.

PLATE XX.

FIG. 1. A vertical section of the cochlea of a 14 mm. foetus from the center of that organ. The course of the fibres in the modiolus is well shown. The characteristic shrinkage in the size of the nerve-bundle after leaving the ganglion is given, and the appearance of the ganglion in cross-section as stained with the silver method is that commonly found in these preparations, but does by no means convey a truthful idea of natural conditions. At *a*, one hair-cell, two supporting cells, and some of the nerve branchings in the Sauropsid organ are shown; *b* shows the branching nerve better, while *c* does the same for the supporting cells; in *d* and *e* the Cortian organ and the nerves running to it are shown; non-nervous parts in outline. Htnk. obj. ½ of 2 Obh. camera.

FIG. 2. A single cochlear canal and its ganglion and nerves from a section similar to the above, more highly magnified. At *h*, three outer hair-cells and their relations to the nerve fibres indicated. The continuity of one nerve fibre and hair-cell is shown.

FIG. 3. Surface view of a portion of the Sauropsid organ showing the continuity of the nerve fibre and sensory cells.

FIG. 4. A portion of the nerves included between the cochlear ganglion and the outer hair-cells. With this magnification the connections of the radial nerves with the spiral bundle are not clearly defined. In the region of the lamina the aberrent fibres do not occur in bundles. Three ganglion cells and numerous sheath cells occurring as varicosities are shown. Htnk. obj. 2 Obh. cam.

FIG. 5. A portion of the arch of Corti with five inner hair-cells with their nerves. The elements of Corti's arch are stained a rusty brown, while cells and nerves are completely black. Htnk. obj. 5 Obh. cam.

FIG. 6. Six ganglion cells from the cochlear ganglion. These are all multipolar cells save one "×," which is a double ganglion cell. Htnk. obj. 5 Obh. cam.

FIG. 7. About one quarter of a complete turn of the cochlear lamina, showing the appearance and relations of the constituent parts of the nerve plate of the lamina. Near the ganglion one notices suboval spaces free from nerves; these spaces later on are occupied by bone. The nerve fibres run both ways from the ganglion. The spiral bundles of fibres appear as complete with this power. A few hair-cells are sketched in, but only such detail is put down as could be introduced into a drawing on this scale. Htnk. obj. 2 Obh. cam.

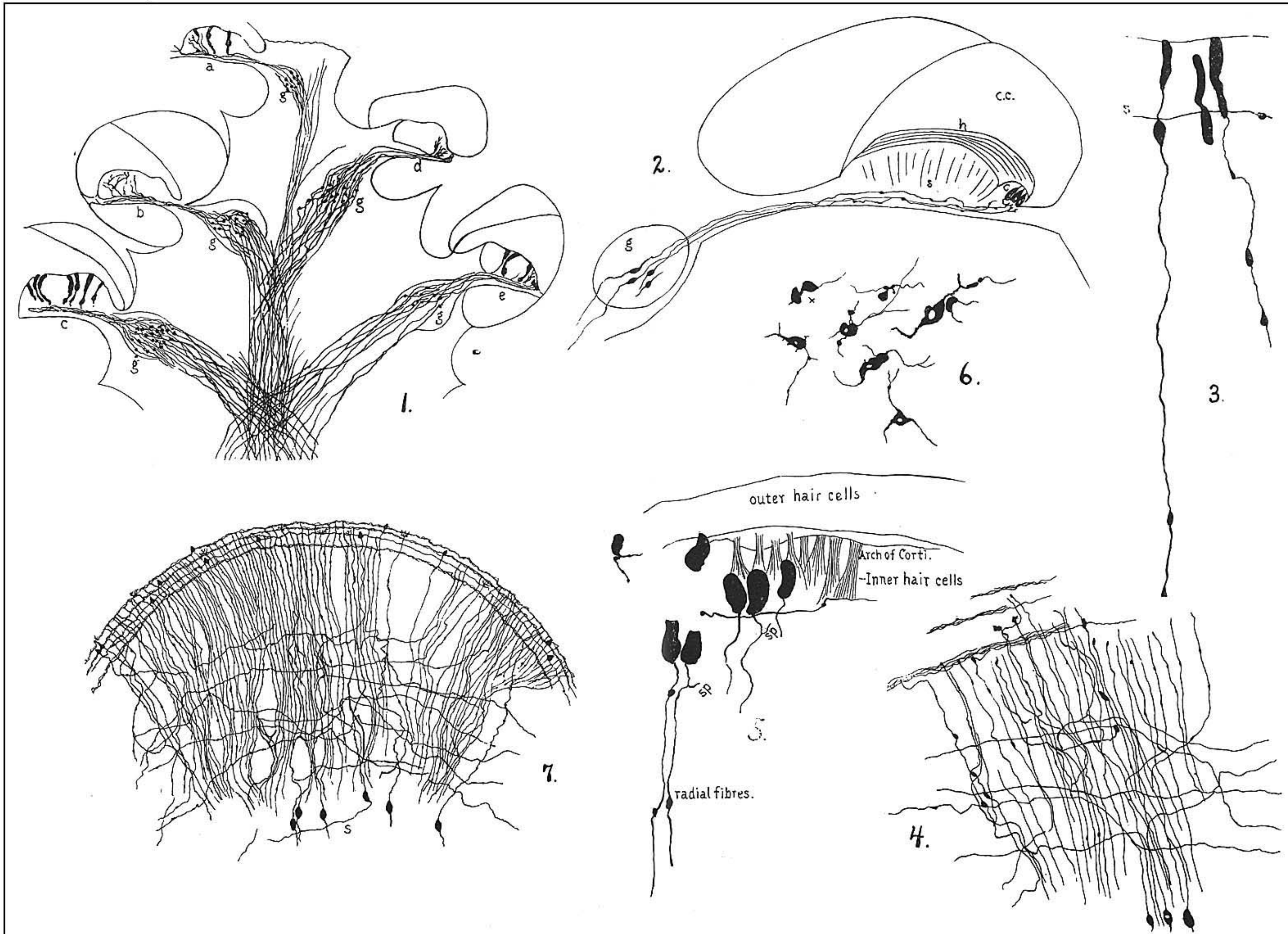

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PLATE XXI.

FIG. 8. A surface view of the cochlea of a 14 cm. foetus showing the nerves from the ganglion to the organ of Corti. The hair-cells are not stained and consequently the stain is incomplete. Htnk. obj. 5, Obh. cam.

FIG. 9. The peripheral portions of a few of the nerves from the last preparation more highly magnified, to show the manner of branching of the nerve end among the hair-cells.

FIG. 10. Two hair-cells and their nerves with a third fibre leaving unusually large varicosities. Htnk. obj. 5, Obh. cam.

FIG. 11. A surface view of a portion of the plexus of nerves in the Cortian organ. One fibre is seen to bend off and enter the spiral bundle.

FIG. 12. A single ganglion cell having three peripheral processes and one central process. Htnk. 5.

FIG. 13. A multipolar cell from a 14 cm. embryo, with four peripheral processes. Htnk. obj. 4, Obh. cam.

FIG. 14. Two cells from the Macula sacculi of a 14 cm. foetus with their nervous prolongations. Htnk. obj. 5, Obh. cam.

FIG. 15. A hair-cell from the second row of outer cells and its nerve. Three rows of stained hair butts indicating the position of the other hair-cells. Htnk. obj. 5, Obh. cam.

FIG. 16. Three hair-cells from the Macula sacculi of a 14 cm. foetus one of them showing the nerve continuity. Htnk. obj. 5, Obh. cam.

FIG. 17. Two nerve fibres and their hair-cell terminations some of which are not stained out to the cells themselves. Htnk. obj. 5, Obh. cam.

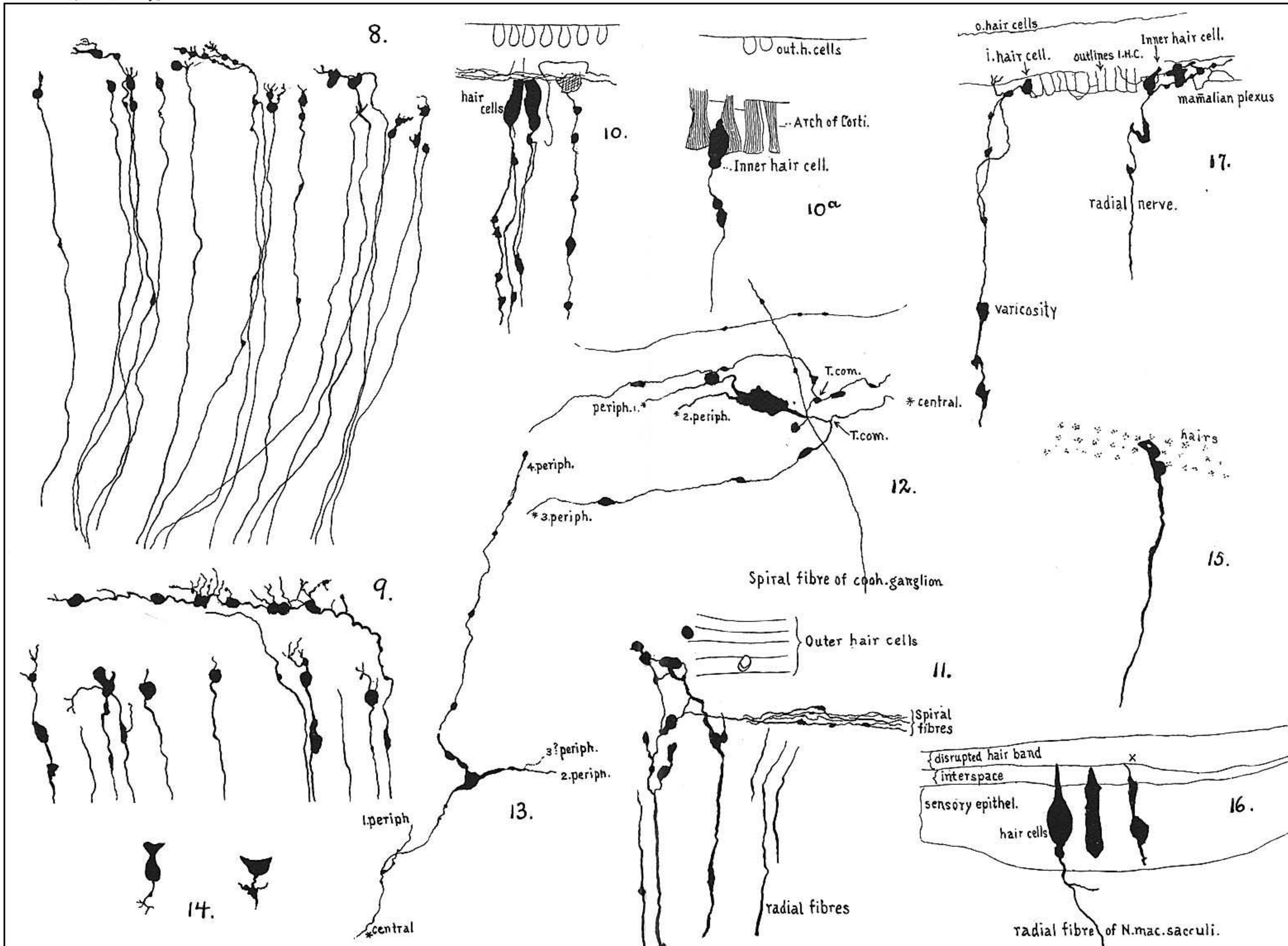

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PLATE XXII.

FIG. 18. Shows the character of the radial fibres between the ganglion and organ of Corti and illustrates the manner in which they may become for a greater or less distance spiral in course. Htnk. obj. 2, Obh. cam.

FIG. 19. A portion of the nerve plate from the lamina of a 10 cm. foetal ox to illustrate the mixing or anastomosing of the fibres of the nerve bundles between the ganglion and organ of Corti. Htnk. obj. 4, Obh. cam.

FIG. 20. Two end brushes of nerve fibres ending in the Sauropsid organ. The points of importance are the large varicosities (group of sheath cells) which the fibres possess just before breaking up into the terminal branches, Htnk. obj. 5, Obh. cam.

FIG. 21. Three supporting cells from the Sauropsid organ and two nerve fibres, which as stained, show in the one case an oval terminal body brown in color, and in the other case only a free end. Htnk. obj. 5, Obh. cam.

FIG. 22. Part of the nerve plate between ganglion and organ of Corti to show branching fibres. Fibre 3 has a varicosity from which is given off a collateral 3^{i} which in turn gives off one of its own 3^{ii} while the main trunk of 3 is continued to the hair-cell at 3. The collateral given off from 3^{i} divides into three terminal branches or more correctly it gives off two other collaterals 3^{iii} 3^{iv} while it is continued to a hair cell not shown in the preparation. Fibre 2 under goes one divison as does fibre 1. Htnk. obj. 4, Obh. cam.

FIG. 23. A single radial nerve fibre which from a triangular enlargement gives off two processes one of which divides into two. These three processes extend to the peripheral organ. Htnk. obj. 5, Obh. cam.

FIG. 24. A surface view of the organ of Corti showing one row of inner hair-cells and five rows of outer hair-cells. The fifth row is not continuous, but suffers frequent interruptions. Htnk. obj. 4, Obh. cam.

FIG. 25. Surface view of a part of the network of nerve fibres in the Cortian organ at the base of the hair-cells. *p* the fibre which proceeds to the ganglion.

FIG. 26. A view from above of the upper surface of the Cortian organ the focus being on the arch of Corti. One outer hair-cell is stained and is connected with an inner hair-cell, equally well stained, by a nerve fibre which crosses the Cortian tunnel somewhat obliquely. Owing to the point of view the nerve appears to pass through the inner hair-cell, whereas it passes below it. Htnk. obj. 5, Obh. cam.

FIG. 27. Part of two commissures or connecting nerves lying just below, *i. e.*, in contact with the bases of the hair-cells of two inner rows of the outer series, showing the characteristic enlargements and the numerous delicate processes which are given off sometimes from the fibres, sometimes from the swellings. At *x* is shown the bundle of fibres lying below the inner row of hair-cells, which forms the most pronounced bundle of the so-called spiral nerves. A part of this structure is shown more highly magnified in the next figure. Htnk. obj. 5, Obh. cam.

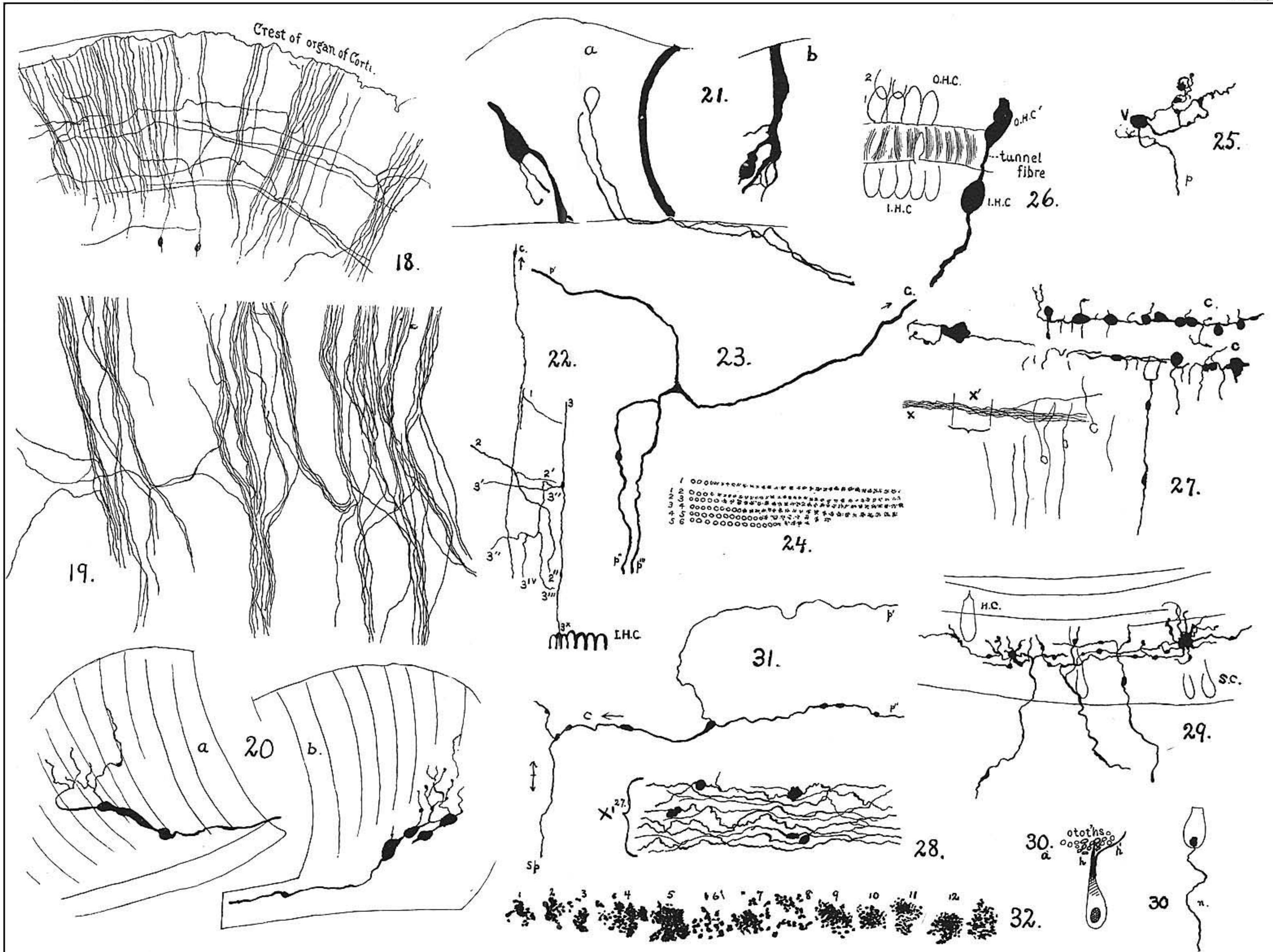
FIG. 28. The bundle of nerve fibres associated with the inner hair-cells to show the nature of the fibres, which are extremely fine filaments. Leitz, obj. 12, Obh. cam.

FIG. 29. A portion of the nerve supply of the macula sacculi, with one of the peculiar ganglionic bodies found in the epithelial layer and the final branchings of the radial nerves, forming horizontal fibres, the homologues of the spiral fibres of the cochlea.

FIG. 30. (*a*) A hair-cell from the macula sacculi, with nerve end in the cell; (*b*) a hair-cell with its hair bent by the contraction of the tissues and of the otolithic mass. Htnk. obj. 5, Obh. cam.

FIG. 31. To show the branchings of a spiral fibre in the neighborhood of the ganglion. Htnk. obj. 5, Obh. cam.

FIG. 32. The habenula perforata of a young dog (16 days), showing the manner of entrance of the nerves into the cochlear canal and the absence of circumscribed foramina nervina. Surface view of the region after removal of the organ of Corti. Htnk. obj. 8, 160 mm. d. t. Obh. cam.



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